Rhodora

JOURNAL OF

THE NEW ENGLAND BOTANICAL CLUB

Vol. 42. December, 1940. No. 504.

A CENTURY OF ADDITIONS TO THE FLORA OF VIRGINIA

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(*Continued from page 498*)

Part III. Phytogeographic Considerations

In 1937 I published[21] a brief analysis of the diverse geographic affinities of the flora of the Coastal Plain of Virginia. At that time I suggested seven primary types of relationship there displayed; these should perhaps be reduced to six. The main groupings, however, seem to hold. During the succeeding years considerable additions have been made to most of the groups; and during the five trips from June to October, 1939 (excluding obviously introduced weeds), we were able to extend into Virginia a great number of ranges: 11 plants of the upland (chiefly Blue Ridge, Appalachian Valley and Alleghenies) new to the Coastal Plain; 20 heretofore unrecorded from north of North Carolina; 9 unknown north of South Carolina; 6 unknown north of Georgia; and 1 heretofore known only in Alabama. Giving us a station or stations to fill in the previous broad gap between North Carolina and isolated areas in Delaware, Maryland or New Jersey are 6 species; while 2 supply an intermediate area between South Carolina and the North, and 4 species were found which had heretofore been known only from the Mississippi Basin or the Gulf States. New southern limits were established for 14 species: 13 the first from south of New Jersey, Delaware,

[21] Rhodora, xxxix. 465–489 (1937).

Maryland or the Potomac near Alexandria, 1 the first from south of southern New England. The Asiatic *Aneilema Keisak* is new to the American flora. *Desmodium glabellum* has apparently been unknown since its original collection in the 18th century in South Carolina. One species, erroneously identified, drops from the Virginia list; and 22 plants new to science, 7 of them endemic in Virginia, were discovered or worked out from earlier collections. Still others await fuller study.

It is needless here to discuss in detail most of the geographic relationships of these plants. They fit, for the most part, into the groupings already discussed. It is gratifying, however, to see regular increase in the group of species which apparently radiated out from the Appalachian Upland as it became elevated from its coastal plain status of Cretaceous time; and to see the gradual reduction in number of the species isolated from North or South Carolina in Delaware or New Jersey. One group of species, those of the fresh or but slightly brackish tidal shores and marshes has not previously been considered in this series of papers. It may, therefore, be specially discussed.

The Flora of Fresh Tidal Estuaries and Shores.—The peculiarity of the fresh or barely brackish tidal estuary[22] is the regular action of tide, alternately flooding and leaving bare the inner shores of streams and inlets twice a day with essentially fresh water. The plants which can tolerate such daily changes are a limited number. Besides the regular and somewhat indifferent species of reed-marsh they consist of a remarkable group of species of a few paludal genera, the species or the genera usually exhibiting as a regular feature of their geographic distribution extreme localization. Although a few plants found in our more brackish estuaries, like *Spartina cynosuroides* and *Scirpus robustus*, tolerate considerable salinity and usually follow the outer coast, the more typical estuarine species are intolerant of much salinity in the waters and confine themselves to the fresh to but slightly brackish reaches of streams, pools and inlets. This group is, then, of peculiar interest, since the plants have apparently mostly attained their present habitats and extreme isolation in the past, at periods when they could

[22] See Fassett, N. C.: *The Vegetation of the Estuaries of Northeastern North America.* Proc. Bost. Soc. Nat. Hist. xxxix. no. 3 (1928).

migrate from river to river along fresh or brackish (not strongly saline) shores.

Such conditions today prevail in a region like Back Bay in southeastern Virginia, where the off-shore bars and continuous dunes of the outer shore shut in a shallow body of tidal waters, perpetually renewed by fresh streams or seepage, and with the nearest inlet from the open sea far below the Virginia-North Carolina line. Rarely, during wild storms, sea-water dashes from the outside Atlantic into sheltered Back Bay; and sufficient salinity has been preserved in some of the marshes to maintain a few specially tolerant halophytes. The shores of Back Bay and the fresh pools and ponds on its margins or on Long Island are, however, the homes of such notable plants of the fresher marshes and waters as *Cyperus haspan* var. *americanus* (MAP 9), the American representative of a pantropical species (tropical and warm-temperate North and South America, Africa and warmer regions of Asia and Australia). The world-range of the species is suggestive of that of *Cyperus brevifolius* (MAP 21). Other typical plants of the freshish marshes of Back Bay are endemics of the two Americas; such, for instance, as *Typha truxillensis* (MAP 8), with details of distribution somewhat different from those of the two species of *Cyperus* and an ability, through its coma of perianth-bristles, to spread, locally, away from the slightly brackish marshes (where it rarely persists). Others are endemics of the southeastern United States. A good example is *Juncus megacephalus* (MAP 5), a very distinct species which occurs in the fresh to brackish marshes from Texas to the shores of Back Bay. Its habitats, as given on such labels as clearly indicate them, are as follows: ditch (La.), wet sandy shores (Fla.), mucky ground (Fla.), flatwood ponds (Fla.), prairie (Fla.), pineland (Fla.), low pinelands (Fla.), moist pine barrens (Ga.), low ground back of sand-dunes (Ga.), lime-sinks (Ga.), savannah (S. C.), dune-hollows (S. C.), river-marsh (S. C.), salt meadow (N. C.), marsh (N. C.), dune-hollow (Va.), swale back of dunes (Va.), inner border of brackish to fresh marsh (Va.). In brief, *Juncus megacephalus*, like its associates, is not a pronounced halophyte; we do not find it, like *J. Roemerianus*, for instance, following the salt marshes. It is not a plant of the saline outer coast but rather of the fresh to barely brackish inner

margin of the coast, sometimes in fresh inland habitats. With great stretches of fresh to slightly brackish inner shore, now extending from below Cape Henry to Cape Fear and, formerly, doubtless more continuously to Florida, it has been able to follow more or less without interruption its most favorable habitats; but it does not follow north along the saline outer coast.

Not all the American plants of Back Bay shores have so continuous a range on the inner coast as do *Cyperus haspan* var. *americanus* and *Juncus megacephalus*. As pointed out on p. 371, the remarkable little genus *Lilaeopsis* (formerly called *Crantzia*) is a living relic of a very ancient dispersal (MAP 7), with its species variously scattered in New Zealand, southeastern Australia, Tasmania, temperate and subtropical South America, the Andes, Mexico and southern Arizona, and Pacific and Atlantic temperate North America. Apparently this disruption of the genus is the result of breaking down of old connections, with Eurasia and Africa omitted. It is difficult not to consider it a remnant of an old spread northward from ancient Antarctica. A frequent species of the Atlantic margin of North America is *L. chinensis* (name reflecting a geographic misconception by Linnaeus), with dispersal in fresh to brackish estuaries from Florida to western Nova Scotia. It is in many estuaries of Virginia. The specialty of Back Bay, however, is a much larger species with matted creeping and floating stems, *L. carolinensis* (MAP 6). On the southeastern side of Long Island in Back Bay a small pond at the head of fresh marsh is filled by this species, a very distinct member of the genus, with its chief center on the lower reaches of La Plata River in temperate eastern South America, but with four remote stations known in North America: near New Orleans; shallow water near Myrtle Beach, South Carolina; an unidentified station (presumably near Wilmington), North Carolina; and this pond on Long Island. *Lilaeopsis carolinensis* doubtless occurs in other shallow waters along or near the inner coast, back of the outer rim of sand dunes, but its two areas, one in latitudes 30°–36° 35′ north, the other between latitudes 25° and 35° south, were presumably derived from a former more continuous large area. In this connection the range of *Triglochin striata* (map 19), with a subantarctic dispersal, on Chatham Island and in New Zealand, Australia,

South Africa, temperate South America and warm-temperate North America (in eastern South America found between lat. 22° and 40° south, in eastern North America between lat. 22° and 38° north), comes to mind, for *Triglochin striata* is known in Virginia only from the tidal marshes of Back Bay. It here accompanies *Ammannia Koehnei* (MAP 4). This is one of the most localized of estuarine plants. Discovered prior to 1840 on the marshes of Hackensack River in northern New Jersey, the species is now known on the estuary of York River and on Back Bay (an endemic variety on one river-estuary), with two known stations (doubtless many more) on the off-shore bar of North Carolina, the other known stations in Florida and locally along the Gulf of Mexico. Like so many estuarine species its range is interrupted. It is, therefore, significant that it belongs to another genus of somewhat general pantropical and warm-temperate range. As stated by Koehne in his treatment of the *Lythraceae* (in Engler's *Pflanzenreich*), *Ammannia* has 20 species, occurring in Australia, the Malayan region, Polynesia, southeastern and southern Asia (extending thence into southeastern Europe and the Mediterranean), Africa, subantarctic Sandwich Islands, South America and the warmer regions of North America. *Ammania* is not a holarctic genus. Like so many others which stretch northward into warm-temperate North America the genus today is primarily tropical and it also shows an austral disruption suggesting an old Antarctic dispersal.

In brief, the species which characterize the fresh to but slightly brackish shores and pools about Back Bay are largely plants of highly restricted and localized occurrence, and they belong for the most part to genera or species with the characteristically severed geographic occurrence of all pantropical and subantarctic groups. Their primary dispersal, considering the fact that they are incapable of succeeding in highly saline habitats, such as prevail on most coasts, has been a phenomenon of the past. Only on landlocked coastal shores can it now go on, except when the plants are transported by man or by the rarest of natural agencies. Of course, when a plant like "Wild Celery", *Vallisneria americana*, intentionally transplanted as a food for waterfowl, is placed in so favorable a habitat as Back

Bay it will prosper. But the plants which give significance to the flora of the region, *Cyperus haspan* var. *americanus*, *Juncus megacephalus*, *Lilaeopsis carolinensis*, *Triglochin striata* and *Ammannia Koehnei*, are largely unnoticed by those who look upon conservation of the wild life of such an area primarily as the attraction and maintenance of waterfowl. There is no probability that the typical estuarine species have been recently introduced by man.

The peculiarly significant indigenous plants of the fresh to but slightly brackish shores of Back Bay are not alone species of tropical and austral groups. Some plants of boreal dispersal are also isolated there. On the seeping, springy sands bordering Back Bay west of False Cape there is a remarkable turf, occupying the fresh springheads and saturated sands. It consists of a close mat of a few species: *Eleocharis albida* (tropical American, here near its northern limit), *E. halophila* Fern. & Brackett (Newfoundland and Gulf of St. Lawrence southward, here at its isolated southern limit), *E. Lindheimeri* (Clarke) Svenson (northern Mexico and San Bernardino Mountains, with distant stations eastward and northeastward to Texas and Michigan, here remotely isolated) and other local plants Among them is the very definite *Ranunculus hederaceus*, a matted herb of springy ground. *R. hederaceus* occurs in western Europe, and its American stations[23] are remote. By early authors, with no field experience with the plant, it was assumed to be an introduction from Europe. This may sometimes be the case. In Newfoundland[24], however, it occurs with the regular indigenous species of wet sands; and, surely, on the shores back of False Cape, where it forms part of the mat, it seems as indigenous as the endemic American species of *Eleocharis* with which it grows or as the highly localized and endemic *Ludwigia brevipes* (New Jersey and southeastern Virginia) which abounds, along with the subtropical *Bacopa Monnieria*, on the neighboring flat. In the Great Dismal Swamp, likewise, it is not in an area where man would presumably carry it. The significance of *Ranunculus hederaceus* in the problem will later be discussed.

[23] See Drew, W. B.: *The North American Representatives of Ranunculus, § Batrachium*, Rhodora, xxxviii., especially pp. 12–14 (1936).

[24] See Fernald, *Some Relationships of the Floras of the Northern Hemisphere*, Proc. Internat. Congr. Plant Sci. ii., especially p. 1506 (1929).

Back Bay, which today presents ideal conditions for the local spread of species of fresh to brackish shores, is not like the typical fresh river-estuary. The fresh estuaries are found far up-stream from the mouths of the eastern Virginian rivers. Those which have been explored by us are on the James and the Chickahominy and their tributaries, on the Pamunkey, the Mattaponi, and, to a lesser extent, on the Nottoway and the Blackwater. They are highly developed but only slightly explored (and that some years ago) on North Landing River. On the main River James the best of the fresh tidal marshes begin about 50 miles from its mouth and thence extend 25 miles up-river, but the smaller tributary creeks and the Chickahominy have good tidal marshes from near their mouths well up-stream, on the Chickahominy at least to Windsor Shades. The York is salt for more than 30 miles, up to Westpoint, at the confluence of the Pamunkey and the Mattaponi. The fresh tidal marshes on the Mattaponi follow that stream (often with broad tidal-marsh islands) about 30 miles, to the region of Walkerton. On the Pamunkey they are finely developed but we have not determined their extent. The Nottoway and the Blackwater unite at the North Carolina line to form the Chowan in North Carolina, reaching the sea via Albemarle Sound, which itself merges into Pamlico Sound, these sounds mostly cut off from the open Atlantic by a wonderful development of off-shore bars, sometimes 4 miles broad. Tidal conditions extend slightly into Virginia on the Nottoway; on the Blackwater they extend above Franklin. North Landing River, a sluggish tributary of Currituck Sound, thence to the sea through Albemarle and Pamlico Sounds, is bordered nearly its whole length by broad and fresh tidal marshes. Its mouth is more than 60 miles from the first opening to the Atlantic, at Oregon Inlet, on the outer coast of Dare County, North Carolina. The fresh tidal estuaries to which I am referring, are, then, anywhere from 30 miles (York River system) to 125 miles (Blackwater River) from the open Atlantic. They illustrate, very typically, the estuaries of Atlantic North America north to the St. Lawrence. On several or all of the Virginian estuaries examined a few of the species of Back Bay are found: *Sagittaria falcata* Pursh (Guatemala to Delaware and Maryland); *Cyperus haspan* var. *americanus* (MAP 9,

already discussed); *Eleocharis albida* (see p. 508) and *Lippia nodiflora* (tropical America, north to Texas, Oklahoma, southeastern Missouri and southeastern Virginia). The river-marshes, however, have a considerable restricted flora, which we do not know on Back Bay. This includes

Isoëtes saccharata (tidal mud of Delaware, Maryland, District of Columbia, and Potomac waters to Alexandria and vicinity.—*Pfeiffer,* Mon. Isoëtaceae; southeastern Virginia, closely approaching North Carolina. See p. 406).

Sagittaria subulata (tidal mud, Alabama and Florida to southeastern Massachusetts).

Zizaniopsis miliacea (Tropical America, north to Maryland and southeastern Missouri).

Echinochloa pungens, var. coarctata Fern. & Grisc. (tidal marsh, North Landing River, endemic).

Cladium jamaicense (tropical America, north to marshes of North Landing River).

Cyperus brevifolius (pantropical, north to Florida and southern Georgia; Chickahominy and Delaware Rivers. See pp. 395 and 419 and map 21).

Rhynchospora macrostachya var. colpophila (tidal marshes of Maryland and Virginia).

Eriocaulon Parkeri (tidal mud, St. Lawrence River; Penobscot River, Maine, to Blackwater River, Virginia. See p. 432 and map 17).

Aneilema Keisak (eastern Asia; southeastern Virginia, closely approaching North Carolina. See p. 441 and map 20).

Cassia fasciculata var. macrosperma (fresh tidal marshes and shores, southeastern Virginia, endemic. See p. 455 and plate 635).

Aeschynomene virginica (fresh to brackish tidal marshes and shores, southern New Jersey, southeastern Pennsylvania and eastern Maryland to the valley of the James. See Rhodora, xli. 466 and map 1).

Hypericum mutilum var. latisepalum (Florida to Texas; fresh tidal marshes of Mattaponi River. See pp. 402 and 466).

Elatine americana (chiefly on tidal mud, St. Lawrence River and interruptedly to Virginia. See p. 466 and map 18).

Ammannia Koehnei var. exauriculata Fern. (marshes of North Landing River, endemic).

Ludwigia alata Ell. (tidal marshes, Louisiana to Florida, thence very locally to North Landing River).

Eryngium aquaticum (Texas to Florida, north to New Jersey. See pp. 386 and 467).

Lilaeopsis chinensis (tidal marshes, Florida to Nova Scotia. See pp. 391 and 470).

BACOPA CYCLOPHYLLA (tidal mud, Florida to Maryland, with apparent gaps of hundreds of miles. See p. 402 and MAP 22).
B. OBOVATA Fern. (tidal mud, Chickahominy river, very rare. See MAP 24).
LOBELIA ELONGATA Small (tidal marshes, very localized, Georgia to Delaware and Maryland. North Landing River and tributaries).
BOLTONIA ASTEROIDES var. GLASTIFOLIA (fresh tidal marshes and shores, southern New Jersey to Louisiana. See pp. 396 and 486 and PLATE 641).
BIDENS MITIS (Michx.) Sherff (tidal marshes, Louisiana to Florida, thence, very interruptedly, to Maryland. North Landing River).

These 22 plants, which, in Virginia at least, are strictly estuarine, are for the most part members of wide-ranging genera; but, whereas some of the more notable plants of the fresh to brackish shores of Back Bay have relatively continuous ranges northward, though others are with strikingly isolated stations, practically all the truly estuarine plants are highly localized. Two of them perhaps persist as relics from former semi-cosmopolitan ranges. *Cyperus brevifolius* (MAP 21) has as wide a range as *C. haspan* (see p. 419), occurring rather generally in the warmer parts of Asia (even north to southern Kamtchatka), the Malayan region, islands of the Indian Ocean, eastern Australia, New Zealand, Oceanica, locally in Africa, on islands of the South Atlantic, and from La Plata River in eastern South America northward to Bermuda and southern Georgia, with isolated stations on the Chickahominy and the Delaware and, westward, in Central America, Mexico and southern California. The world-range is definitely of the pantropical order, with the suggestion of radiation out of ancient Antarctica. Those who know the plant in eastern Asia and the Malayan region, however, state that it is there inclined to become a weed. On the Delaware it has not long been recognized and we have only a single station as yet on the Chickahominy. That is below an old ferry-landing, where it is not impossible that the plant started from oriental packing or straw thrown away. It needs further watching before we can surely assert that it is indigenous on the Chickahominy and the Delaware.

The other species of remote geographic relationship is *Aneilema Keisak* (MAP 20). It is so definitely a part of the regular vege-

tation of river-shores and fresh tidal marshes throughout the area from the Mattaponi to the Blackwater, always with the endemic and highly conservative eastern American estuarine species, that it is most difficult to think of it as a possible introduction. It seems as indigenous as the local *Cassia*, *Aeschynomene* and *Rhynchospora* with which it associates and as *Phryma*, *Liriodendron*, *Carya* and the other woodland genera which occur only in eastern North America and eastern Asia. When MAP 20, showing the range of *Aneilema Keisak*, is compared with MAP 21, giving the range of *Cyperus brevifolius*, one can not fail to recognize that it is like two small segments of MAP 21, with the rest of the world eliminated. It must be noted, however, that the very recent discovery of *Aneilema Keisak* in America at first seems like an argument against its being indigenous. When, however, we consider that such an abundant and very conspicuous plant of drier (therefore more accessible) areas of southeastern Virginia as the gigantic sunflower-like herb, *Silphium compositum* (up to 10 feet high and with leaves often a foot broad) was long overlooked as a Virginian, until within the past decade[25], that the regular estuarine companion of *Aneilema Keisak*, *Aeschynomene virginica* (up to 8 feet high, with ornamental pea-like flowers), was not known as a living Virginian from the time of its discovery by Clayton two centuries ago until Long and I found it in 1938, or that the very conspicuous and usual companion of these, the abundant endemic large-fruited *Cassia* (up to 6 feet high and with showy orange-yellow flowers) was undetected until 1939, the fact that the Aneilema has only recently been discovered in America becomes a very unimpressive point. Most of the phytogeographically significant plants of tidewater Virginia were unknown there a decade ago. It is most interesting, therefore, that *A. Keisak* occurs exclusively with conservative and endemic American estuarine species in southeastern Virginia and not in rubbish, waste spots, roadsides or man-made ditches. If it is not a native it has assumed a remarkable resemblance to one. It should not be overlooked, on the other hand, that another Asiatic species of *Aneilema* is found on the Coastal Plain from Florida to South Carolina. This is *A. nudiflorum* (L.) Wallich[26] of southern Asia, which

[25] See Fernald, RHODORA, xxxix. 329 (1937).

[26] For statement of nomenclatural situation see Merrill, Journ. Arn. Arb. xviii. 65 (1937).

Small (*Manual*) cites from "Roadsides, woods, and orange-groves, Coastal Plain, Fla. to Ga. Nat. of E. Indies." Not only is *A. nudiflorum* native of the East Indies; Clarke, in his monograph, says "India Orientalis, Malaya, China; ab Himalaya ad Zeylaniam, Borneo, ins. Philippine et Loo-Choo; alt. 0–2000 met., vulgatissima". I do not know its status in Florida and Georgia, except from the statement of Small; but the only Floridan label in the Gray Herbarium with statement of habitat reads "low flat woods", while Neil Hotchkiss, writing of its occurrence on Minim Island, Santee Delta, Georgetown County, South Carolina, said "the plant appeared to be at home along the margin of a marsh"[27]. That suggests the behavior of *A. Keisak* in southeastern Virginia. Both plants must be watched. Tidal marshes are scrupulously avoided by all except the most hardened of botanists; and even though *A. nudiflorum* may be a recent adventive from Asia which is rapidly spreading, *A. Keisak* may prove to be, as its behavior suggests, a conservative and ancient member of our flora.

There is no question that the remaining 20 species which in Virginia are restricted to fresh river-estuaries are indigenous. They include many phytogeographic types: some are tropical American species, like *Cladium jamaicense* ("Saw-grass"), reaching their northern limit on streams entering Currituck Sound, or *Zizaniopsis*, which comes farther north; others, like *Ludwigia alata*, are strictly North American but unknown in Virginia except along North Landing River; others, like *Eryngium aquaticum* or *Lobelia elongata*, are primarily southern but reach New Jersey, Delaware or Maryland; while some, such as *Sagittaria subulata* and *Lilaeopsis chinensis*, are scattered from the southeastern states to southern New England or Nova Scotia. Another series is prevailingly northern. *Eriocaulon Parkeri*, MAP 17 (member of a pantropical group of probably ancient dispersal from Antarctica), is on the fresh tidal mud of the St. Lawrence from above to far below Quebec, on tidal marshes of New England, New York, New Jersey, Delaware, Maryland and Virginia; while *Elatine americana* (MAP 18, excluding reported stations in the interior of the continent) is on the tidal reaches of the St. Lawrence, and on remote tidal muds from

[27] Hotchkiss, RHODORA, xlii. 21 (1940).

Northumberland Strait, New Brunswick, to the James, the known areas often 100 to 200 miles or more apart. Others, like *Isoëtes saccharata* and *Aeschynomene virginica* are chiefly on tidal marshes of the Delaware system and those confluent with Chesapeake Bay; *Rhynchospora macrostachya* var. *colpophila* belongs in the tidal marshes of the Chesapeake area in Maryland and Virginia; *Cassia fasciculata* var. *macrosperma* is endemic in tidal marshes from the Mattaponi to the James; and three others are known only from a single series of tidal marshes each: *Echinochloa pungens* var. *coarctata* and *Ammannia Koehnei* var. *exauriculata* on North Landing River and *Bacopa obovata* Fernald (MAP 24) on the Chickahominy.

If we were to follow northward, investigating the specialized floras of the different fresh tidal estuaries, we should find these conditions repeated: *Bidens bidentoides* on the Hudson, Delaware and Maurice (New Jersey) Rivers; *B. mariana* Blake on Northeast River and the lower Susquehanna in Maryland; *B. Eatoni* (with many localized and recognizable varieties along separate rivers) in the marshes of far-distant rivers from the St. Lawrence to the Hudson; *B. infirma* Fernald endemic on the St. Lawrence; *Micranthemum* (or *Hemianthus*) *micranthemoides* from the lower Hudson to the Potomac; *Cardamine Longii* Fernald (MAP 24) on tidal mud of Cathance River, Maine; *Gentiana Victorinii* Fernald (map 20) and *Cicuta Victorinii* Fernald on the St. Lawrence; and so on with several others. Whether primarily southern and failing to reach north to Virginia, or barely entering the state, or known northward to the Potomac, the Susquehanna or the Delaware; or more northern and known from the James or the Blackwater to the Penobscot or the St. Lawrence, the estuarine flora shows undoubted localization within the narrow ecological limits in which it thrives. Furthermore, specific or varietal endemism is a regular feature of this flora. Restricted endemics, known from no other area, are found in the marshes of more than a dozen rivers from southern Virginia to the St. Lawrence; and from Maine to Virginia they show a marked preference for the smaller rivers and creeks with extensive swales, rather than the larger. In Virginia, so far as we yet know, the endemics of a single (rarely also on an adjacent one) river are on the North Landing River, the Chick-

ahominy and the Mattaponi, not on the James, the Rappahannock and the Potomac. This is evidently due to the much greater development of marsh along the small streams (the larger rivers, like the James, having more open wave-washed and unstable shores) and to their naturally more circumscribed areas (the larger rivers tending to have a more generalized flora).

When we consider the genera to which the species belong it will be seen that they are all wide-ranging or subtropical or tropical groups. The strictly holarctic genera are not represented. This fact, that the estuarine species belong in genera of semi-cosmopolitan, subtropical, tropical or extreme austral occurrence (*Eriocaulon* and *Lilaeopsis*, for instance) is of importance, for we do not get estuarine floras well developed on the more northern areas of eastern North America. The St. Lawrence and the streams entering the Gulf of St. Lawrence are, apparently, the northernmost rivers with well developed estuarine floras, but from there to North Carolina and beyond the estuarine floras become significant to the student of the flora.

I have sufficiently emphasized the extreme isolation of these plants and their very limited tolerance of other conditions than those in which they grow. By some their dispersal, whether they be pantropical types or endemic American species, is satisfactorily explained by saying "the birds did it", just as by a geologist of some renown I am told that the famous isolation of Coastal Plain plants about the head of Lake Michigan is wholly explained by the presence there of a bustling commercial center, Gary, freight-cars and railroad-engines, to his mind, having transported the seed. Not having the imagination to visualize railroad-trains dipping down into the Coastal Plain bogs and pools to secure the seeds of rare species of *Psilocarya* and other highly localized paludal and aquatic conservatives, in order to plant them (many milleniums before Gary was ever thought of) in the bogs and pools of northwestern Indiana, I can hardly be satisfied by so simple an explanation. So, cognizant of the many studies showing that migrating birds fly clean and that they are such expert aviators as not to carry on their long flights adhering chunks of mud to unbalance them, and that they eat most plants as food, not as altruistic spreaders of remote epibiotics, I can accept the superficial and too easy explana-

tion that birds are the chief agents which have brought about the present ranges of many plants, only in case of their very short flights and flutterings from one spot to another in close proximity. If birds have been the primary agents in dispersing our most conservative estuarine species, it seems very strange that we should have so many limited endemics, known only from the shores of single or of few rivers. As has been repeatedly shown, the overworked bird is scarcely to be taken seriously in this problem.

So, likewise with winds. The plants which characterize the estuary-flora are those of wet mud, inundated shores and drowned marshes. They are not plants of dry habitats. If seed-bearing portions get stranded and sufficiently dry to be picked up by wind, this must be a rare exception and not enough to account for the regular occurrence in so many fresh estuaries of the same species. The seeds of estuarine species rarely, if ever, have modifications to favor wind-dispersal.

I have shown how, along such an extensive landlocked area as Back Bay, spread of the shore- and marsh-plants is a simple mechanical process, and that such a species as *Juncus megacephalus*, intolerant of much salinity, occurs back of the off-shore bars, islands and dunes, very regularly from Pamlico Sound to Back Bay. Although its two nearest relatives, *J. scirpoides* and *J. brachycarpus*, plants of stable sands, peats and clays and of more inland occurrence, follow north, in the former case to southern New York, in the latter to the local Tertiary beds of Massachusetts, *J. megacephalus* of fresh to but slightly brackish marsh stops its northern spread abruptly at Back Bay, beyond which the coast becomes open and exposed to the full saline influence of the Atlantic[28]. Right here, I believe, is the explanation of the great isolation in our fresh tidal river-estuaries of the distinctive plants of warm-temperate, subtropical, tropical and subantarctic relationships. These plants are intolerant of the extreme salinity of outer coasts; they thrive in the area between high and low tide where the waters are at most only slightly brackish. They are an extremely conservative and fastidious element in our flora. The wide latitudinal range of this special-

[28] Extensive landlocked bays farther north, like Chincoteague, Sinepuxent and Assawoman Bays, extending from Accomac County, Virginia, to Sussex County, Delaware, may, when properly explored, yield many of these southern species. Who knows?

ized flora along the margin of the northeastern United States and Canada, from southeastern Virginia (some of the species from Florida and the Tropics) to New Jersey, southern New York, the tidal rivers of Maine or even of eastern New Brunswick and, in some cases, the St. Lawrence from Lake St. Peter to below Quebec, calls for a condition comparable with that of Pamlico, Albemarle and Currituck Sounds and Back Bay today. Most geologists are agreed, I believe, that such a condition existed, all the way from Florida to the Gulf of St. Lawrence, when the continental shelf, now submerged off our Atlantic coast, was elevated as a nearly continuous outside ridge. That would make a tremendous southwest to northeast landlocked sound along the borders of which plants of fresh to merely brackish tidal shores could freely travel, just as today they are swashing and spreading on the changeable marshes and shores of Back Bay. The shores need have been no more stable than are those of Back Bay today; the exact stations of the plants need not have been fixed. The quality of the shore, tidal and fresh to brackish, not strongly saline, was the essential to success. To me this seems the obvious explanation. With the depression of the continental shelf the coast, especially northward, lost its outer fringe, the shores were bathed directly by seawater and the long stretches of country between the fresh tidal reaches of the rivers and creeks lost the estuarine flora. It today exists as a relic of the period before the continental shelf became depressed.

In considering when this migration northward along the landlocked sounds which extended to the Gulf of St. Lawrence, took place it is pertinent to quote from the thoughtful study of our coast by Professor Douglas Johnson. From his New England-Acadian Shoreline[29] I quote:

> In Georgia and Alabama, exclusive of the Florida projection, that part of the Atlantic coastal plain exposed above sealevel has a breadth of 150 to 175 miles; in the Carolinas and Virginia it narrows to 125 miles or less; in New Jersey it declines from 65 to 25 miles; in Long Island, Marthas Vineyard, and Nantucket it appears as narrow fragments only; and off the coast of Maine is wholly lost to view. At the same time the submerged portion of the coastal plain, forming the continental shelf, which off southern Florida is only a few miles wide,

[29] Johnson, Douglas, The New England-Acadian Shoreline. New York, John Wiley & Sons. 1925. See especially pp. 296–302.

broadens off the Carolinas and Virginia to 50–80 miles, reaches a breadth of 100 miles off northern New Jersey, and where wholly submerged off the coast of Maine has a width of 150 miles or more. The increase is not uniform, however, for the submerged part of the plain is unusually broad opposite the bight where Florida and Georgia meet, and unusually narrow in the Cape Hatteras region. At the southwest the inner lowland, where well developed as in Alabama, is far from the sea. In the Virginia-New Jersey sector it dips under the water in places, is slightly but continuously submerged in Long Island Sound, and deeply so in the Gulf of Maine. Could we have a more striking picture of a single great topographic belt 150–200 miles broad, submerged progressively deeper and deeper toward the northeast, one of its elements after another disappearing from view, until all are completely buried under the ocean?.

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It will appear from this table [not here included] that the margin of the Atlantic continental shelf (excluding the Bahama banks) is only a few fathoms below sealevel off Florida, is from 25 to 35 fathoms deep off Georgia and the Carolinas, 40 to 48 fathoms opposite Maryland, 48 to 55 off the New Jersey and Long Island coasts, and 60 to 70 fathoms deep at the outer edge of the Banks. There are some local departures from the gradual deepening toward the northeast; but the progressively greater submergence in this direction, indicated so clearly by the progressive drowning of the cuesta and lowland topography and by the narrowing of the exposed coastal plain toward the northeast, is strikingly confirmed by the attitude of the edge of the continental shelf.

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It would seem that the depth of the Gulf of Maine inner lowland offers us the most reliable measure of the amount of submergence of this coast that we thus far possess. The unreliable character of estimates based on depths of submarine channels, especially when the subaërial origin of those channels is still open to question, has been commented on in another connection. But in the broad inner lowland of a coastal plain, preserving on its floor features characteristic of subaërial denudation operating on coastal plain deposits of unequal resistance, we apparently have a safe basis for calculation. Unless tidal scour has been strongly operative,—and both the form of the bottom and other considerations would seem to dispose of the possibility of effective tidal erosion on the broad open floor of the inner basin,—we have in the maximum depth of the drowned lowland a minimum measure of submergence since the lowland was carved. Several soundings between 180 and 200 fathoms are found along the deep channel at the northern base of the main cuesta. That these particular depths cannot be ascribed to tidal scour is indicated by the fact that the outlet channel farther east, between Georges Bank and Brown Bank, is much shallower. We must rather infer partial filling of the former valleys in cuesta and lowland, due possibly to slumping from the Banks and to material removed from their summits by waves and currents. Streams doubtless flowed from the deep areas in question through the outlet channel to the former sea margin many miles to the southeast; hence the apparent submergence calculated from the

soundings must be increased by an allowance for the fall of the stream. It seems safe to say that since the inner lowland now forming the Gulf of Maine was carved, the land has been submerged to a depth of more than 1200 feet. If the land recently stood several thousand feet higher than now, as some have believed, it must have been for a very short period only; else the inner lowland, drained by a stream trenching comparatively weak coastal plain deposits, would have been graded to a much lower level. Farther to the southwest, as already noted, the submergence was progressively less than in the Gulf of Maine region, although there is evidence that the decrease was irregular, with local areas of increasing submergence,—facts which show that a subsidence of the land rather than a rise of sealevel was primarily responsible for the submergence.

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The interpretation of the Banks as a coastal plain cuesta receives support from the fact that in the course of their operations on the Banks fishermen bring to the surface fragments of fossiliferous sandstone and limestone. A series of these collected and described by Upham, and determined by Verrill to be of Tertiary age, (probably Miocene or even Pliocene) shows that the submergence must have occurred at the end of the Tertiary or still later in post-Tertiary time; for after the deposition of the late Tertiary sediments we must allow time for the erosion of the lowland prior to its submergence. If the bevelled top of the cuesta is the remnant of a peneplane developed on the coastal plain beds (and perhaps also on the crystallines of the oldland), then since the deposition of the late Tertiary formations the land was uplifted, one cycle of erosion completed, another uplift occurred, and in the new cycle maturity was attained before subsidence drowned the resultant topography. Thus we should expect the subsidence to be at least post-Miocene, and more probably post-Pliocene.

With this picture, so graphically presented by Douglas Johnson, of the northward depression of the Coastal Plain until, from Massachusetts eastward, it was completely submerged (except for the relatively slender and rapidly disintegrating Sable Island at the outer rim, more than 100 miles south of Cape Breton Island), it is easy to see what happened to the flora of fresh to but slightly brackish shores which, as I view the problem, freely spread along the margin of the landlocked sound which, by the final submergence of the Banks Cuesta in "post-Miocene, and more probably post-Pliocene" was finally severed into scattered remnants.

The interpretation that the conservative plants of the estuaries of New York, New England, New Brunswick and the St. Lawrence from Lake St. Peter to below Quebec can have persisted somewhere in those regions through the Wisconsin glaciation is distasteful to many who still hold to the archaic idea that

Wisconsin glaciation eliminated all life from these areas. So many evidences exist indicating that with us the Wisconsin was a relatively weak phase of Pleistocene activity as compared with earlier ice-accumulations, and so many conservative animals and plants are now found in regions where it is most improbable that they have arrived, without leaving traces of their migrations, since the Wisconsin, that I find myself not at all disturbed. My views and much of the evidence on this question and the phenomenal bulk of parallel evidence accumulated by Nordhagen, Hultén and others in Scandinavia and elsewhere in Eurasia and in Alaska are presumably well known. They need no expansion here. The evidence added by the isolated colonies of estuarine plants lingering in New York, New England, New Brunswick and Quebec is a slight but important addition to the whole story.

I have referred to *Ranunculus hederaceus* of wet sands of western Europe acting like a native on wet sands, tidal shores and about spring-heads in southeastern Newfoundland and on scattered points southward to Back Bay. It is simply one of many species which share western Europe and eastern America, especially Newfoundland. That considerable flora includes plants of mossy woodlands, acid bogs and other strictly natural habitats, plants which do not tolerate and can not spread by means of salt water. In addition to these plants numerous freshwater and land snails of native and undisturbed habitats show similar ranges. These and other cases, including some higher animals, are so numerous that it is absurd to imagine that they have been swimming the Atlantic in post-Wisconsin time, to find the natural habitats of Newfoundland, Gaspé and other areas within the latitude of Wisconsin glaciation. Their occurrence and their pre-Wisconsin spread has elsewhere been discussed and need not now divert us. *Ranunculus hederaceus* as well as *Carex arenaria* on the sands of Cape Charles may well be members of this illuminating group.

With this discussion of the disrupted floras of fresh tidal shores I close the paper. Their study is only begun. Thousands and thousands of miles of shores of fresh to merely brackish sounds and bays and hundreds and hundreds of fresh tidal river-estuaries from Florida to Delaware are botanically un-

known. They will yield many new endemics. As I have repeatedly said, there is plenty to do; there are few botanically equipped and with energy or initiative to do it.

NOTES WITH EXTENSIONS OF RANGE OF SEVERAL NORTH AMERICAN ORCHIDS.—In the course of identifying American orchids, chiefly in the Herbarium of Oberlin College, there appeared the following collections of several species which constitute interesting extensions of range:

× HABENARIA ANDREWSII White ex Niles. (*H. psycodes* × *H. lacera* and *H. psycodes* var. *grandiflora* × *H. lacera*.)

This natural hybrid, which occurs from eastern Canada through New England and New York south to North Carolina, now appears in the middle West.

OHIO: Oberlin, South woods, June 27, 1890, *J. B. McCord s. n.* (Herb. Oberlin Coll. 71736).

HABENARIA CILIARIS (L.) R. Br.

This widespread species of the Atlantic coastal plain and the middle West is here recorded from Wisconsin. Albert M. Fuller (in Studies on the Flora of Wisconsin, Pt. 1: Orchidaceae Bull. Pub. Mus. City of Milwaukee 14 (1933) p. 46) says: "In 1838, Dr. I. A. Lapham listed it (H. ciliaris) for the Milwaukee region. . . . There has been no other record for this species in Wisconsin. The nearest station where authentic specimens of this species have been found, is Calumet, Cook County, Illinois."

WISCONSIN: May 30, 1891, *R. M. Strong s. n.* (Herb. Oberlin Coll. 26232).

HABENARIA CLAVELLATA (Michx.) Spreng.

Heretofore the northwestern limit of this widespread orchid appears to have been Minnesota. It now appears from the Rocky Mountain region.

MONTANA: Helena, *F. W. Anderson s. n.* (Herb. Oberlin Coll. 26444).

EPIPACTIS LATIFOLIA (L.) All.

Until recently this common European species has apparently been restricted to the eastern part of Canada and the eastern United States. Lately it has appeared in the West.